

GAS EXCHANGE AND PHOTOSYNTHETIC ACTIVITY IN *Hancornia speciosa* GOMES SEEDLINGS UNDER WATER DEFICIT CONDITIONS AND DURING REHYDRATION

TROCAS GASOSAS E ATIVIDADE FOTOSSINTÉTICA EM MUDAS *Hancornia speciosa* GOMES SOB ESTRESSE HÍDRICO E DURANTE A REIDRATAÇÃO

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ABSTRACT: Considering the wide distribution of *Hancornia speciosa* Gomes in the Brazilian savanna, environment with irregular distribution of rainfall, it is believed that their seedlings can be cultivated for a few days under water restriction, information that can stimulate the use of this species in restoration or planting for sustainable exploration programs. The present study evaluated the gas exchange and photosynthetic activities of *H. speciosa* seedlings and examined their tolerance to water deficit and their metabolic recovery after rehydration. We evaluated the photosynthetic rate, internal carbon concentration, transpiration rate, stomatal conductance, water-use efficiency, photosystem II quantum efficiency (Fv/Fm), instantaneous carboxylation efficiency, chlorophyll index, and recuperation potential of *H. speciosa* seedlings after rehydration. Twelve month-old seedlings were used and maintained at 70% of their soil water retention capacity. Data was collected 7, 10, 12, 14, 16, 18, 20, 23, 31, 33, 35, 37, 42, 44, 46, and 48 days after suspending irrigation; irrigation was reinitiated when the photosynthetic rate approached zero. Water deficit conditions reduced all of the parameters evaluated except the chlorophyll index; stressed seedlings required 42 days for the photosynthetic rate to reach zero, but photosynthetic equilibrium was reestablished just five days after rehydration. This temporary water deficiency did not cause any permanent deleterious effects on the photosynthetic apparatus of the seedlings.

KEYWORDS: Brazilian savanna. Stress. Native fruit tree. Mangaba.

INTRODUCTION

The species *Hancornia speciosa* Gomes (family Apocinaceae), locally known as "mangaba", is a native tree found in southeastern, central-western, northern, and northeastern Brazilian. Its fruits are very delicious and have high nutritional value, being consumed *in natura* or used to make juices, dried fruits, jams, syrups, wines and vinegar (BARROS et al., 2010; SANTOS et al., 2010). The populations of this typical species of the Cerrado biome (Neotropical savanna) have been drastically reduced due to anthropogenic impacts. The general situation of abandonment and poor treatment of "mangaba" trees has been partially alleviated by the efforts of some farmers to establish structured plantations of these trees in response to the high demand and high prices of their fruits (SOUZA et al., 2007). However, very little information is currently available about the ecophysiology of the seedlings of this species. Thus, research on techniques for cultivation or production of seedlings

may encouraging the planting for sustainable exploration.

Water deficit tolerance mechanisms have been examined in various plant species, and the results of these analyses have been applied to speed recovery within degraded areas and in seedling production. Plants in arid and semi-arid regions are frequently exposed to water deficits, which negatively affect plant growth and productivity (WU et al., 2008; ZHANG et al., 2011). Plants can avoid stress via maximizing water absorption by deepening their roots, or by minimizing water loss via stomatal closure (KOZŁOWSKI; PALLARDY, 2002). These morphological and physiological responses can lead to stress adaptation, but can vary considerably among species (SOUZA et al., 2004).

Water stress leads to reduced leaf water reserves, which is associated with a limited transpiration rate (BAQUEDANO; CASTILLO, 2006) caused by stomatal closing. This, in turn, reduces internal CO₂ availability, declining the plant's photosynthetic ability (PARRY et al., 2002; MEDRANO et al., 2002; CALBO; MORAES,

1997; SOUZA et al, 2004; SINGH; SINGH, 2006; OSIPOVA et al., 2011).

Studying water stress and the plants' ability to recover contributes to a better understanding of the plants' potential to adapt to different environments and climatic conditions. Recovery is an important component of plant responses to drought, and carbon balance depends not only on the rate and degree of photosynthetic decline under a water deficit but also on the capacity of recovery of photosynthesis after water is supplied (CHAVES et al., 2011; FLEXAS et al., 2004, 2007; MIYASHITA et al., 2005).

Considering the extensive distribution of this species within the Brazilian savanna environment with irregular rainfall distribution, its seedlings can grow for a few days under water restriction. The present study evaluated the gas exchange and photosynthetic activities of *Hancornia speciosa* Gomes seedlings and examined their tolerance to water deficit and their metabolic recovery after rehydration.

MATERIAL AND METHODS

The experimental procedures described here were undertaken under greenhouse divisions at the Faculdade de Ciências Agrárias da Universidade Federal da Grande Dourados (UFGD), located in the municipality of Dourados, Mato Grosso do Sul State (MS), Brazil (22°13'16"S x 54°17'01"W; at 430 m a.s.l.). The regional climate is classified as cwa (MATO GROSSO DO SUL, 1990), with a mean annual rainfall of 1500 mm and a mean annual temperature of 22 °C.

Hancornia speciosa Gomes ("mangaba") seedlings were produced from seeds derived from a native Brazilian savanna population in MS. The seedlings were cultivated in polyethylene recipients (5 kg capacity) in a substrate composed of 50% red distroferic latosol and 50% de sand (v:v), under 30% shading. After 12 months forty seedlings had heights between 15.0 and 18.3 cm, stem diameters of 3.11 to 4.05 mm, 15 to 16 expanded leaves, and primary roots from 25 to 33 cm long.

The growth substrate was hydrated to 70% of its water retention capacity (WRC) and the seedlings subsequently separated into two treatment groups of 20 seedlings divided into 4 repetitions: 1 – Controls, which were irrigated periodically to maintain their 70% WRC; and treatment 2 – characterized by water stress, in which irrigation was suspended until the photosynthetic rates of the seedlings attained near-zero values, at which time daily irrigation was reinitiated. During the

experimental period the seedlings were isolated from natural rainfall in a covered greenhouse.

The photosynthesis ($A - \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$); transpiration ($E - \text{mmol H}_2\text{O m}^{-2}\text{s}^{-1}$); internal carbon concentrations ($C_i - \mu\text{mol CO}_2 \text{ mol}^{-1}$); stomatal conductance ($g_s - \text{mol m}^{-2}\text{s}^{-1}$) of the seedlings were determined using an infrared gas analyzer (IRGA) (model LCi PRO; Analytical Development Co. Ltda, Hoddesdon, UK). The water use efficiency of the plants was calculated using the A/E ratio ($\mu\text{mol de CO}_2 / \text{mmol de H}_2\text{O}$), and the water-use efficiency instantaneous carboxylation efficiency was calculated by the A/C_i ratio ($\mu\text{mol m}^{-2}\text{s}^{-1} / \mu\text{mol mol}^{-1}$). Measurements were performed using the stabilization apparatus, where Δc was adopted as the stabilization criterion.

PS II photochemical quantum efficiency (F_v/F_m) was determined by examining leaves that had been kept in the dark for 20 min using a portable fluorometer (Opti-Sciences, model OS-30p). The leaves were subsequently exposed to a saturating light pulse for 0.5 s ($3000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ intensity).

To avoid the effect of time, the measurements were performed by alternating between the control and stressed plants, where gas exchange and fluorescence data were recorded at the same time.

All measurements were performed between 08:00 and 10:00 on day 7 after suspending irrigation, from a single fully expanded leaf. Five seedlings from each repetition of each treatment were evaluated at 7, 10, 12, 14, 16, 18, 20, 23, 31, 33, 35, 37, 42, 44, 46, and 48 days after suspending irrigation. The irregular intervals between evaluations reflect the need to perform the measurements under similar weather conditions, i.e., sunny days without clouds. The evaluations were completed when the photosynthetic rate approached the initial rate (control).

The data were subjected to analysis of variance, mean values were compared by an F test, and standard deviation was calculated at each point.

Five adult plants growing in a natural environment in Brazilian savanna vegetation in Mato Grosso do Sul State, Brazil, were also characterized in terms of their gas exchange rates after a 30 day period with a total of 69.9 mm of rainfall (source: the meteorological station at UFGD). These plants demonstrated the following parameters: internal CO_2 concentration $244.5 \pm 26.33 \mu\text{mol CO}_2 \text{ mol}^{-1}$; stomatal conductance $0.098 \pm 0.005 \text{ mol m}^{-2}\text{s}^{-1}$; photosynthetic rate $5.94 \pm 1.11 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$; transpiration rate $2.48 \pm 0.8 \text{ mmol H}_2\text{O m}^{-2}\text{s}^{-1}$; instantaneous CO_2

carboxylation efficiency $0.024 \pm 0.004 \mu\text{mol m}^{-2}\text{s}^{-1} / \mu\text{mol m}^{-2}\text{s}^{-1}$; water-use efficiency $2.40 \pm 0.17 \mu\text{mol CO}_2 / \text{mmol H}_2\text{O}$.

RESULTS

During the experimental period, the control seedlings of *Hancornia speciosa* Gomes

demonstrated average photosynthetic rates (A) of $2.29 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Figure 1A). The seedlings exposed to water deficit conditions demonstrated significant variations in their photosynthetic rates during the experimental period, with decreases after the day 18 until the day 42 of evaluation, when this parameter approached zero ($0.125 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and irrigation was reinitiated.

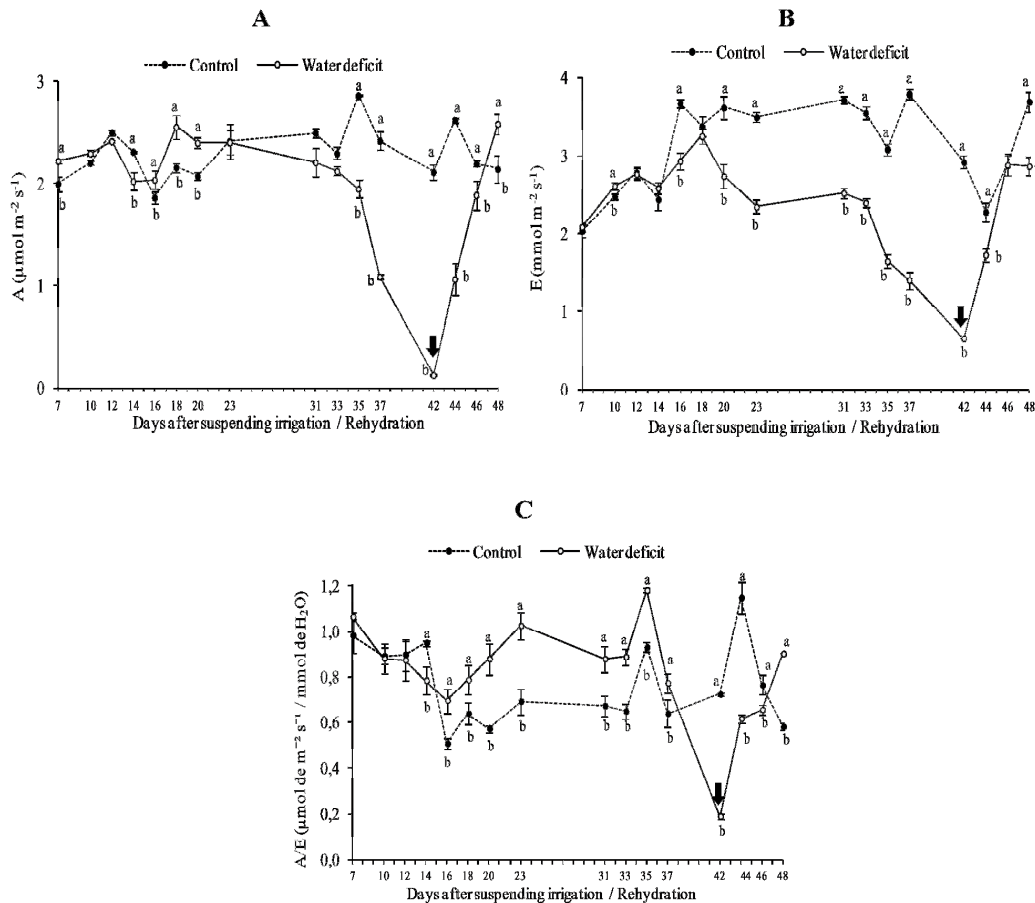


Figure 1. Mean values of the photosynthetic rate (A), transpiration rate (B), water-use efficiency - A/E (C) as a function of the evaluation days among irrigated *Hancornia speciosa* Gomes seedlings submitted to water stress conditions. The arrows indicate the re-initiation of irrigation, and the bars represent the standard errors of the means.

After rehydration, the seedlings that had been exposed to water-deficit conditions rapidly reinitiated their photosynthetic metabolism, with corresponding increases in their photosynthetic rates. They reached control levels by day 47 and a mean of $2.585 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ by day 48, significantly surpassing the photosynthetic rate of the control seedlings. The previously stressed seedlings only required 5 days to recover their initial photosynthetic rates.

The transpiration rates (E) of the stressed seedlings remained very similar to the control

seedlings until the day 14 after suspending irrigation (Figure 1B), after that time, the stressed seedlings showed reductions in transpiration until the day 42 when irrigation was reinitiated, with a mean of $0.665 \text{ mmol H}_2\text{O m}^{-2}\text{s}^{-1}$. Similar to the photosynthetic rate, the transpiration rate recuperated quickly, and after five days of renewed irrigation the seedlings demonstrated values similar to those of the control seedlings ($2.88 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$).

Both treatments had a similar water-use efficiency ratio (A/E) until approximately day 12 of

evaluation, after which the stressed seedlings demonstrated higher water-use efficiency than the controls until approximately day 37 (Figure 1C). The control seedlings had lower mean water-use efficiency ($0.76 \mu\text{mol}$ of CO_2/mmol of H_2O) than the stressed plants ($0.82 \mu\text{mol}$ of CO_2/mmol of H_2O). After day 35 of water deficit, the seedlings exhibited a sharp reduction in A/E, reaching

significantly lower values than those exhibited by the control seedlings at day 42.

The mean of the internal CO_2 concentration (C_i) fluctuated throughout the experiment. It was significantly decreased after day 10 of suspended irrigation, except on days 14, 31, and 44, when it did not differ compared to the control, and then it increased before rehydration (Figure 2A).

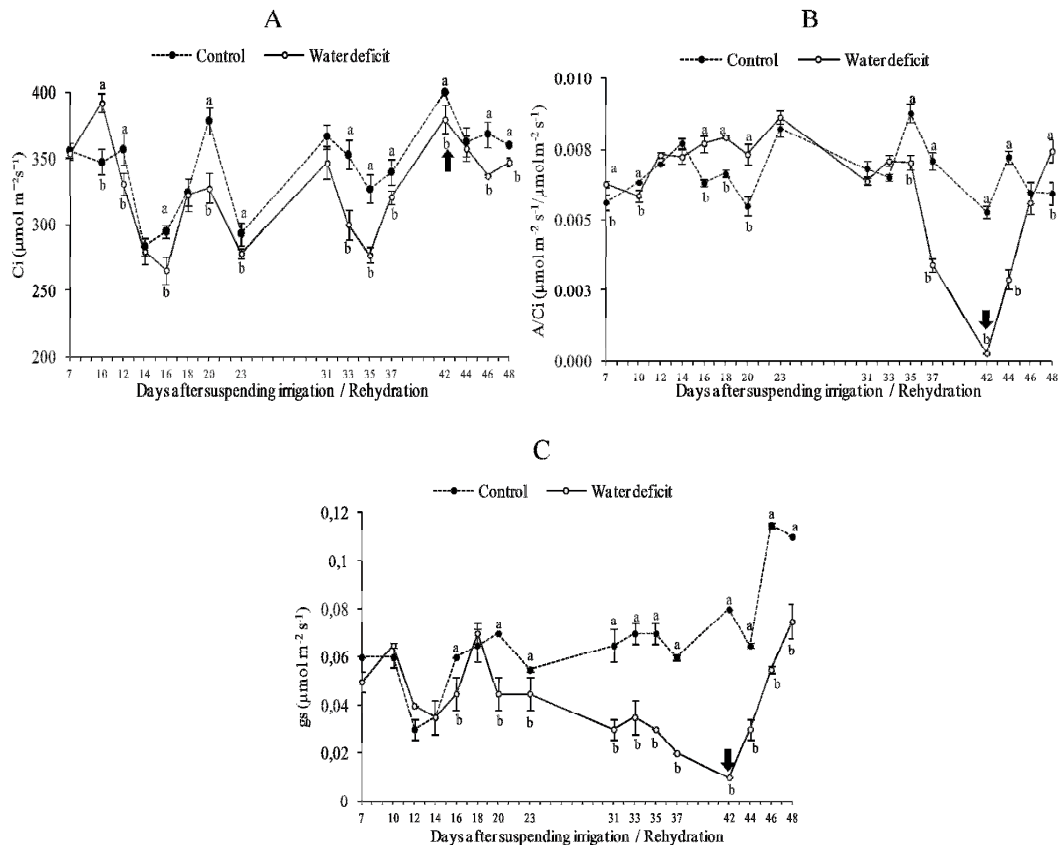


Figure 2. Mean values of the internal CO_2 concentration (A), instantaneous carboxylation efficiency of CO_2 - A/C_i (B) and stomatal conductance (C) as a function of the evaluation days among irrigated *Hancornia speciosa* Gomes seedlings submitted to water stress conditions. The arrows indicate the reinitiation of irrigation, and the bars represent the standard errors of the means.

The mean instantaneous CO_2 carboxylation efficiency (A/C_i) values (Figure 2B) were similar in both treatments in some of the evaluations; however, the water-stressed seedlings demonstrated a pronounced decline after day 35. The stressed plants exhibited rapid recovery after rehydration, reaching control values by day 46 of evaluation.

Stomatal conductance (g_s) only differed between the treatments after day 14 and was low in seedlings exposed to water-deficit conditions, remaining significantly lower from day 18 onward (Figure 2C). Stomatal conductance recovered with rehydration, reaching levels only slightly lower than that of the control.

It could therefore be seen that with the reinitiation of irrigation the seedlings showed recuperation of their photosynthetic rates, transpiration levels, stomatal conductance, and CO_2 carboxylation efficiency by rubisco in only five days.

The PS II photochemical quantum efficiency (F_v/F_m) of the control seedlings demonstrated wide variation, with a mean of 0.77 (Figure 3), but remained significantly higher than the stressed seedlings until day 37, when the stressed seedlings exhibited a pronounced decline in F_v/F_m , reaching a mean of 0.7. PS II photochemical quantum efficiency decreased in the plants exposed

to water deficit, reaching a mean of 0.70 on day 42, then increasing by day 48, but not returning to the

initial level.

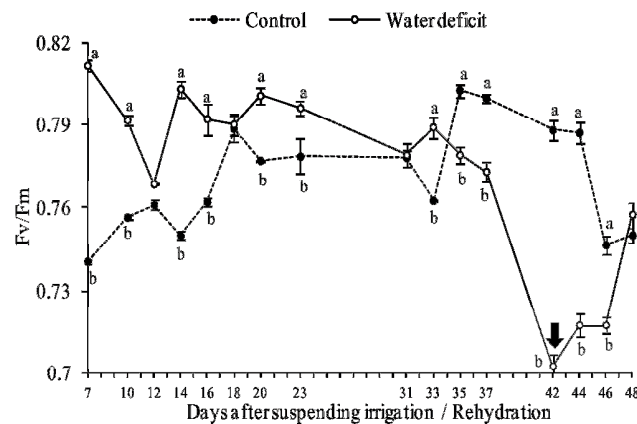


Figure 3. Mean values of the PS II photochemical quantum efficiency as a function of the evaluation days among irrigated *Hancornia speciosa* Gomes seedlings submitted to water stress conditions. The arrows indicate the re-initiation of irrigation, and the bars represent the standard errors of the means.

DISCUSSION

The reduced stomatal conductance became more pronounced at around day 10 after suspending irrigation, and the reduced transpiration rate became more pronounced after day 18, decreasing faster than the photosynthetic rate after day 23.

Reduced stomatal conductance did not appear to be the main cause of reduced photosynthetic rates in stressed *H. speciosa* seedlings, as their internal carbon concentration remained similar to the controls. However, the observed reduction in g_s was certainly responsible for reduced transpiration rates that remained low until day 42 of evaluation, when the photosynthetic rate approached zero and irrigation was reestablished.

Stomatal conductance fluctuated until day 18 after suspending irrigation, with subsequent gradual reductions until day 42, although the internal CO_2 concentration remained high until irrigation was suspended. This behavior suggests that other factors are involved in controlling photosynthesis.

A decline in stomatal conductance usually indicates either partial stomatal closure due to reduced leaf water content and dehydration of the guard cells or a hormonal response, one of the first lines of plant defense against soil-water deficiency. Although leaf Ψ_w was not evaluated, there are reports in the scientific literature showing that controlling stomatal opening in water-deficient plants seems to be an immediate response to low water availability in the soil (ARCOVERDE et al., 2011; POMPELLI et al., 2010; SILVA et al., 2010;

FLEXAS et al., 2006) even before a decrease in the relative leaf water content is noted.

In their review of the literature, Sapeda et al. (2013), found a strong evidence that g_s responds to soil moisture content more than leaf turgor; therefore, reduced stomatal conductance under water stress conditions may be unrelated to reduced leaf moisture content (POMPELLI et al., 2010; SILVA et al., 2010; ARCOVERDE et al., 2011), but it may be related to other factors such as the plant hormone abscisic acid (ABA) (WILKINSON; DAVIES, 2002) which originates from the roots and functions to minimize water loss due to transpiration.

Although stomatal closure should be a rapid response that reduces water loss, increasing resistance to CO_2 diffusion in the mesophyll, carboxylation efficiency is only affected after reduced stomatal conductance. Veiga e Harbermann (2013) it was observed that carbon assimilation was dependent on g_s but not on C_i in unwatered plants. In their review article, these authors have highlighted that the water potential of the soil does not reach very low values in deeper layers during the dry season; however, g_s , the CO_2 assimilation rate, and the transpiration rate decreases.

As such, the observed reductions in the photosynthetic rates of water-stressed seedlings can be attributed to reductions in stomatal conductance associated with the reduction of rubisco CO_2 carboxylation efficiency; reductions in A/C_i in *H. speciosa* only became strongly pronounced after the day 35 of evaluation, however, when there was also a major decrease in the photosynthetic rate. According to Medrano et al. (2002), Parry et al.

(2002) and Flexas et al (2006) drought conditions reduce mesophyll metabolism by diminishing the activation and activity of rubisco carboxylase. Reduced rubisco efficiency can be caused by increased mesophyll resistance due to stomatal closing, thus restricting the absorption of CO₂ by the chloroplasts and possibly increasing the action of rubisco oxygenase and, consequently, photorespiration.

Results similar to those reported here for *H. speciosa* have been observed in other species. Stomatal responses to water deficit conditions in genotypes of *Spondias tuberosa* Arruda ("umbu") suggest that stomatal closing represents the first line of defense against desiccation (SILVA et al., 2009). The recuperation of photosynthesis, transpiration, and the water potential in *Bactris gasipaes* Kunth ("pupunha") seedlings was observed three days after reinitiating irrigation, while stomatal conductance only increased by 50% in that same period (OLIVEIRA et al., 2002). Recuperation of 70% conductance five days after reestablishing irrigation was reported by Calbo (1996) in *Mauritia vinifera* Mart. ("buriti"), and 90% recuperation after 14 days in *Euterpe oleraceae* Mart. ("açazeiros"). The internal CO₂ concentrations of *Mauritia vinifera* Mart. ("buritizeiro") were found to remain more or less constant, without any obvious direct relationship with stomatal conductance (CALBO and MORAES, 1997).

The water-use efficiency of water-stressed *H. speciosa* seedlings was generally greater than that of controls during the period when the photosynthetic and transpiration rates became reduced (between the day 16 and 37 after suspending irrigation), although their water-use efficiency diminished with increasing stress after the day 37, as the lack of available water produced more intense reductions in the transpiration rate (reaching near-zero levels by the day 42). The metabolic processes reinitiated after rehydration, leading to an increase in this ratio due to significant increases in the photosynthetic rate in relation to transpiration.

Rocha and Moraes (1997) noted similar responses in *Stryphnodendron adstringens* (Mart.) Coville to those reported here for *H. speciosa*, with increases in water use efficiency when stomatal conductance and transpiration were lowest. Both species are probably well adapted to low water conditions, as water-use efficiency is defined as the quantity of CO₂ fixed even while the plants are actively limiting water losses. As such, the greater the ratio of CO₂ fixed to water lost, the greater the water-use efficiency of that plant.

Regarding PS II photochemical quantum efficiency, despite Fv/Fm not achieving full recovery until day 42 of evaluation, the water-deficit conditions experienced by the stressed seedlings did not cause irreversible damage to the photosynthetic apparatus (with a mean of 0.77) or the photochemical system (CHAVES et al., 2011). Plants with intact photosynthetic apparatuses have maximum chlorophyll fluorescence values (Fv/Fm) between 0.75 and 0.85 (BOLHAR-NORDENKAMPF et al., 1989; MAXWELL; JOHNSON, 2000), and any decrease in this ratio reflects photo-inhibitory damage to the PSII reaction centers (BJÖRKMAN; DINMING, 1987; THACH et al., 2007).

The *H. speciosa* seedlings exhibited rapid recovery of all of the characteristics evaluated, except Fv/Fm, within five days after rehydration. Sapeta et al. (2013) reviewed the recovery of the photosynthetic rate after stress depends on stress intensity. After moderate stress, rapid and complete recovery may occur, but after severe stress, complete photosynthetic recovery may take several days to weeks or may not occur (BOYER, 1971; MIYASHITA et al, 2005; FLEXAS et al, 2006; CHAVES et al., 2009, 2011).

The results of the present work indicate that *H. speciosa* seedlings exposed to water stress conditions show reduced photosynthetic activities, reaching near-zero values 42 days after suspending irrigation; this reduction was due to stomatal conductance limitations and low rubisco carboxylation efficiency and not to irreversible damage to photosystem II.

These results suggest that *H. speciosa* seedlings can be cultivated with periods of water restriction in a greenhouse or in areas of recomposition, since the periods of lack of water does not exceed 42 days. Further studies should be carried out under field conditions to assess more accurately how these plants behave when planted directly in the soil and in full sun.

CONCLUSIONS

Water deficits reduced all of the parameters evaluated.

Stressed seedlings required 42 days for their photosynthetic rates to approach zero, but were able to reestablish photosynthetic equilibrium just five days after rehydration.

Water deficits did not cause any deleterious effects on the photosynthetic apparatus of stressed seedlings.

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RESUMO: Considerando a ampla distribuição de *Hancornia speciosa* Gomes no cerrado, ambiente com distribuição irregular de chuvas, acredita-se que suas mudas podem ser cultivadas por alguns dias sob restrição hídrica, informações que podem estimular o uso desta espécie em restauração ou plantio para programas de exploração sustentável. O presente estudo avaliou as trocas gasosas e atividade fotossintética das mudas de *H. speciosa* e sua tolerância à deficiência hídrica e recuperação metabólica após a reidratação. Avaliou-se a taxa fotossintética, a concentração interna de carbono, a taxa de transpiração, condutância estomática, eficiência do uso da água, eficiência quântica do fotossistema II (Fv/Fm), eficiência instantânea de carboxilação, índice de clorofila, e potencial de recuperação das mudas de *H. speciosa* após a reidratação. Foram usadas mudas de doze meses de idade, que foram mantidas sob 70% da capacidade de retenção de água do solo. Os dados foram coletados aos 7, 10, 12, 14, 16, 18, 20, 23, 31, 33, 35, 37, 42, 44, 46 e 48 dias após a suspensão da irrigação, que foi reiniciada quando a taxa fotossintética aproximou-se de zero. A condição de déficit hídrico reduziu todos os parâmetros avaliados, exceto o índice de clorofila; mudas estressadas necessitam 42 dias para que a taxa fotossintética chegue a zero, mas o equilíbrio fotossintético é restabelecido cinco dias após a reidratação. Essa deficiência de água temporária não causou efeitos deletérios permanentes no aparato fotossintético das mudas.

PALAVRAS-CHAVE: Cerrado. Estresse. Árvore frutífera nativa. Mangaba.

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